

Christopher T. Yarnes · William J. Boecklen

Abiotic mosaics affect seasonal variation of plant resources and influence the performance and mortality of a leaf-miner in Gambel's oak (*Quercus gambelii*, Nutt.)

Received: 19 January 2005 / Accepted: 11 July 2005 / Published online: 10 November 2005
© The Ecological Society of Japan 2005

Abstract Conceptual models of terrestrial trophic dynamics have emphasized the potential influence of various abiotic factors, though empirical studies have found generalities to be scarce. Progress may result through an increased use of experimental gradients in tandem with existing, natural gradients of abiotic factors that are more difficult to manipulate. Along an elevation/climatic gradient, a fertilization experiment was conducted to examine the impact of environmentally induced variation in foliar nitrogen on tri-trophic interactions for *Phyllonorycter* sp., a leaf-miner (Lepidoptera: Gracillariidae), in Rocky Mountain white oak, *Quercus gambelii*. Microclimate determined the relative effect of host-plant and natural-enemy effects for *Phyllonorycter* sp. Cooler, more humid microclimates resulted in a higher biomass payoff (total biomass/density). Further, increased seasonal variation in foliar nitrogen content at warmer, drier sites significantly increased parasitism rates. Fertilization treatments increased foliar nitrogen content and resulted in increased early-instar mortality. Fertilization treatment also acted in a non-linear fashion with microclimate to influence spatial patterns in parasitism rates. Overall, microclimate was found to affect characteristics of each trophic level, including host-plant nitrogen dynamics, *Phyllonorycter* sp. performance, and parasitism rates. Additionally, nutrient availability altered patterns of parasitoid-related mortality in *Phyllonorycter* sp. within microclimates. These results suggest that local topographic variation in combinations of abiotic factors, or abiotic mosaics, has important effects for spatial patterns of tri-trophic interactions.

Keywords Environmental heterogeneity · *Quercus* · Leaf-miner · Trophic · Seasonal variation

C. T. Yarnes (✉) · W. J. Boecklen
Department of Biology, MSC 3AF,
New Mexico State University, Las Cruces,
NM 88003, USA
E-mail: chris.yarnes@gmail.com
Fax: +1-505-6465665

Introduction

Abiotic heterogeneity, such as the spatial and temporal distribution of resources (e.g., water, light, CO₂ or nutrients) or environmental conditions (e.g., temperature, wind), can have significant consequences for natural populations both directly (Neilson and Wullstein 1986; Sparks and Ehleringer 1997; Oleksyn et al. 1998; Brewer and Gaston 2002) and indirectly, by increasing variation in the quantities and qualities of interacting organisms (Bryant 1987; Benedict and Hatfield 1988; Dudt and Shure 1994; Reynolds and Crossley 1997; Moon et al. 2000). Recent emphasis has been placed on the role of abiotic heterogeneity in determining the structure and dynamics of trophic interactions in terrestrial ecosystems (Hunter and Price 1992; Price 1992; Preszler and Boecklen 1996; Roininen et al. 1996; Stiling and Rossi 1997; Moon et al. 2000; Yarnes and Boecklen 2005).

Elevation gradients exhibit variation in several biologically important abiotic components. For instance, elevation is known to display differences in nitrogen availability (Neilson and Wullstein 1986; Erelli et al. 1998), as well as climatic variables such as temperature (Oleksyn et al. 1998), relative humidity (Sparks and Ehleringer 1997) and rainfall (Lull and Ellison 1950). These variables can potentially affect ecologically relevant nitrogen dynamics in plants (Xin 1993; Sparks and Ehleringer 1997; Buse et al. 1999). Subsequently, elevation-based differences in climatic variables and nitrogen availability may drive patterns of host-plant quality for herbivorous insects (White 1984; Scriber and Slansky 1981) and possibly affect tri-trophic interactions (Stiling and Rossi 1997).

To date, empirical studies of abiotic effects on herbivore populations have largely focused on single factors, most often nutrient additions. Few studies have examined the cumulative effects of multiple abiotic components on host quality across both spatial and temporal scales (but see Moon et al. 2000; Gaston et al.

2004). This strategy has produced limited knowledge of how abiotic factors act singly or synergistically to produce heterogeneity in the trophic forces that affect sources of mortality for herbivorous insects.

Previous work has described broad-level effects of elevation on *Phyllonorycter* sp., a leaf-mining herbivore (Lepidoptera: Gracillariidae), in *Quercus gambelii* Nutt. (Preszler and Boecklen 1996; Yarnes 2003; Yarnes and Boecklen 2005). The relative importance of top-down and bottom-up forces has been shown to generally shift across elevation, whereby unexplained *Phyllonorycter* sp. mortality increases and parasitism decreases with increasing elevation. However, elevation is a coarse gradient often composed of complex differences in topography and aspect that affect biologically important site-specific characteristics, such as microclimate. Whether previously observed patterns of performance and mortality are due to ambient environmental factors, site-based differences in nutrient availability, or are associated with a combination of abiotic factors is hereto unknown.

We hypothesize that the interactive effects of microclimate and nitrogen availability in *Q. gambelii* are responsible for previously observed patterns of trophic dynamics. We test this hypothesis by imposing an experimental gradient of nutrient addition along a natural gradient of ambient environmental conditions. Specifically, we quantify patterns of co-variation in foliar nitrogen concentrations and a set of environmental variables along an elevation (climatic) gradient under a fertilization regime. We then examine the subsequent consequences for performance and mortality of *Phyllonorycter* sp. associated with *Q. gambelii* in the San Mateo mountain range of west-central New Mexico, USA.

Materials and methods

Study system

Quercus gambelii Nutt. (Fagaceae) is a deciduous montane oak associated with the *Pinus ponderosa*-dominated communities of the Southern Rocky Mountains. *Q. gambelii* occurs at elevations between 1,890 and 2,900 m in central New Mexico. The leaf-mining moth *Phyllonorycter* sp. (Lepidoptera: Gracillariidae; NMSU Arthropod Museum accession no. 26263) is a common lower-surface blotch miner of *Q. gambelii* (see Aguilar and Boecklen 1992). Larval development of *Phyllonorycter* sp. proceeds through five instars. We describe instars 1–2 as “early-instars” and 3–5 as “late-instars” and utilize these descriptions in our analysis. When larvae switch feeding modes (sap feeding to tissue feeding) following the second instar, a readily identifiable change in the orientation of mouthparts occurs along with indicative changes in mine wall characteristics that aids in the identification of developmental stage. Pupation occurs in September and adults overwinter in leaf

litter or the bark of their host. Adults emerge in the spring followed by mating and oviposition. Several species of parasitic Hymenoptera (including Ichneumonidae and Braconidae) are the dominant parasitoids of *Phyllonorycter* sp. Predation by other insects and birds has been observed, but is extremely rare at our sites.

Elevation

In 2001, an elevation transect was established within Rosedale Canyon on the southeast-facing slope of the San Mateo Mountains, Cibola National Forest, in west-central New Mexico, USA. Twenty-one experimental trees were randomly chosen at each of four elevations: 2,192 m (E1); 2,438 m (E2); 2,635 m (E3); 2,866 m (E4). These elevations represent the topographic distribution of *Q. gambelii* within Rosedale Canyon. Trees at each site are 3–5 m in height, of similar DBH and exhibit relatively open canopies.

Fertilization

At each site, trees were randomly assigned a fertilization treatment: control (C)=0 g_N m⁻², treatment 1 (T1)=3g_N m⁻², and treatment 2 (T2)=6 g_N m⁻². T1 and T2 represent a 50% increase and 100% increase, respectively, above estimated nitrogen demand in *Q. gambelii* (V. Gutschick, personal communication). Fertilization treatments were applied in single events at E1 following budbreak on 11 May 2001 and at all other sites on 18–20 May 2001. Solubilized granular ammonium sulfate was applied in a 1-m² donut at a distance of 1 m from the tree, approximately equal to the edge of the canopy. The amount of water applied was equivalent to a 4-mm rainfall event.

Environmental data

HoBo Pro RH/TEMP data loggers were placed at each site in early spring before budburst and removed following herbivore collection at the end of the growing season. Data loggers were affixed to trees at a central location within each site and out of direct sunlight. Daily mean, minimum and maximum values of relative humidity and temperature were determined where 24-h intervals are bracketed by midnight. Sites were grouped through a principal components analysis of the correlation matrix of weekly mean values of environmental data and these groupings were used to create microclimate categories of sites (Yarnes 2003; Yarnes and Boecklen 2005). The first principal component represented a gradient of increasing temperature and concomitant decreasing relative humidity. Sites were then ordinated along the first principal axis; the ordination of sites according to microclimate was not related to site

elevation. Subsequently, we constructed two microclimate categories of sites based upon the ordination (Fig. 1) into “cool, wet” sites (CW; positive first principal component) and “hot, dry” sites (HD; negative first principal component).

Sampling: foliar nitrogen

Leaf sampling for foliar nitrogen began with occurrence of first-instar mines of *Phyllonorycter* sp. and ended at pupation. At each sampling date, five unmined and undamaged leaves were sampled haphazardly from each tree at each site for foliar nitrogen analyses. Care was taken to avoid sun leaves from the outermost canopy to minimize variation in estimates of tree-level nitrogen. Leaves were flash-frozen in the field using liquid nitrogen and subsequently transferred to a freezer and stored at -80°C until analysis. Leaves were sampled on 22 June 2001, 25 July 2001 and 25 September 2001.

Sampling: primary and secondary consumers

Phyllonorycter sp. larvae undergo pupation in late September and leaves were sampled for *Phyllonorycter* sp. on 28 September and 6 October 2001, just prior to the onset of leaf senescence and following pupation at each site. Trees are rarely larger than 4–5 m tall with relatively open canopies and were sampled from the ground. Sampling of larger trees was done using ladders. Each tree was sampled for mined leaves during timed searches of 10 min per tree, resulting in approximately 400 leaves per tree. We utilize the number of mines gathered during these searches as estimates of *Phyllonorycter* sp. density.

Nitrogen analysis

Dumas combustion analysis was used to quantify foliar nitrogen content expressed as percent dry mass. Leaves were dried at 45°C for 48 h and ground to a fine powder. Measurements were carried out at the Laboratory for

Environmental Chemistry, INRAM, Las Cruces, New Mexico using a ThermoFinnigan EA Flash 1112 (CE Elantech, Lakewood, N.J.). A NIST (National Institute of Standards and Technology, USA) peach leaf standard of known nitrogen content was run every 15th sample.

Herbivore performance and mortality

Leaves bearing mines (collected as above) were placed in separate petri dishes, stored at 20°C , and monitored for emergence of leaf-miners or parasitoids (cf. Preszler and Boecklen 1994). At the conclusion of adult emergence, two measures of performance were determined for leaf-miners on each tree: percent emergence for each tree and total *Phyllonorycter* sp. biomass. Leaves with mines that failed were scored for unexplained mortality at sap-feeding (early-instar: first and second instar) or tissue-feeding (late-instar: greater than third instar) stages and parasitism events were recorded.

In this study, we equate unexplained mortality with host-plant effects as is common convention in the leaf-miner literature (i.e., Mopper and Simberloff 1995; Hawkins et al. 1997). There is substantial evidence that leaf-miners are subjected to fewer diseases than external feeders (Conner and Taverner 1997). Additionally, Preszler and Boecklen (1996) documented a low incidence of competitive effects for *Phyllonorycter* sp. on *Q. gambelii* (<2% of leaves bore two or more mines).

Statistical methods

All ANOVA models were analyzed using microclimate category as a fixed effect in place of elevation (site; see “Environmental data” section) with individual sites as replicates nested within microclimates. Seasonal variation (SD) and average tree foliar nitrogen at microclimates were further analyzed using this model.

To determine spatio-temporal variation in tree average foliar nitrogen, a mixed effects repeated-measures ANOVA was performed with site (elevation), treatment

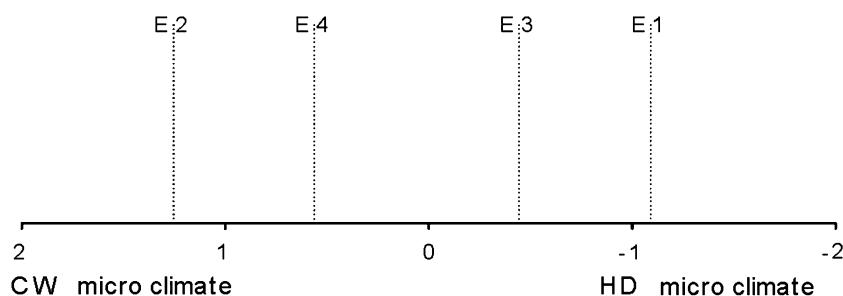


Fig. 1 Ordination of sites along the first principal component axis (x-axis) of environmental parameters during the growing season of 2001. Each point represents the first principal component for each site. Sites with *negative first principal components* exhibited warmer temperatures and lower relative humidity; these were grouped into

a “hot/dry” microclimate (HD). Sites with *positive first principal components* exhibited cooler temperatures and greater relative humidity; these were grouped into a “cool/wet” microclimate (CW). E1 Elevation 2,192 m; E2 elevation 2,438 m; E3 elevation 2,635 m; E4 elevation 2,866 m

(C, T1 and T2), and sampling date (three dates) as fixed effects, and trees nested within sites. Linear contrasts were performed between: sites grouped by microclimate categories, treatments and for dates.

Phyllonorycter sp. density and biomass were analyzed using ANOVA under the model described above. Co-variation of these preference and performance measures, as well as parasitism rate, with measures of host quality [seasonal variation (SD) and average foliar nitrogen] was further analyzed through linear regression. *Phyllonorycter* sp. densities were log-transformed (\log_{10} density + 1) prior to statistical analysis. For each tree, a measure of biomass payoff per female investment through oviposition decisions may be described as the probability of emergence (no. emerged/density) times the average weight of the offspring (cumulative weight/no. emerged). *Phyllonorycter* sp. payoff (in biomass): biomass payoff = $\log_{10}[(\text{cumulative weight} + 1)/\text{density}]$. Leaf-miner emergence across microclimate and treatment was analyzed using logistic regression. Stage of mortality at each microclimate (site) and treatment was examined using contingency table analysis. Logistic regression was used to analyze parasitoid attack for those mines advancing to late-instar stages; parasitoids do not attack the early sap-feeding instars (R. W. Preszler, personal communication). Predictor variables in the full model included microclimate, treatment and the average and seasonal variation of foliar nitrogen for each tree. Contingency table analysis was applied to determine the relative contributions of unexplained mortality (host-plant effects) and parasitism (natural enemy effects) to leaf-miner mortality.

All analyses were carried out using SAS 8.2 (SAS Institute, Cary, N.C.) and considered significant at $\alpha < 0.05$. All ANOVA assumptions were tested and met.

Results

Overall, total foliar nitrogen concentrations in *Q. gambelii* were consistent with those expected for long-lived trees (Mattson 1980). Experimentally, foliar

nitrogen exhibited significant variation across sites and dates, and the interaction of site with treatment, and site and dates (Tables 1, 2). Foliar nitrogen exhibited a slight increase between June and July, with another increase during September when photosynthetic capacity is reduced (Larcher 1995). Seasonal foliar nitrogen dynamics were found to be significantly related to microclimate ($F_{1,74} = 21.636$, $P < 0.001$; Fig. 2), where HD sites experience greater seasonal variation in foliar nitrogen ($F_{1,74} = 21.236$, $P < 0.0001$) and lower total foliar nitrogen ($F_{1,74} = 8.565$, $P = 0.005$; Table 2).

Phyllonorycter sp. densities were lower at CW sites ($F_{1,74} = 6.55$, $P = 0.013$). *Phyllonorycter* sp. density was not related to fertilization regime ($F_{2,74} = 0.286$, $P = 0.752$), average tree foliar nitrogen ($F_{1,82} = 1.77$, $P = 0.187$), or seasonal variation in foliar nitrogen ($F_{1,82} = 1.281$, $P = 0.261$). *Phyllonorycter* sp. biomass payoff was significantly higher at CW sites ($F_{1,74} = 11.072$, $P = 0.001$), yet treatments had no effect ($F_{2,74} = 2.023$, $P = 0.139$). Moreover, payoff does not appear to be related to average foliar nitrogen ($F_{1,82} = 1.473$, $P = 0.228$) or seasonal variation in host nitrogen ($F_{1,82} = 0.718$, $P = 0.399$).

Phyllonorycter sp. experienced greater emergence success (Wald $\chi^2 = 11.015$, $df = 1$, $P < 0.001$) at CW sites, but the timing of mortality (early instars vs. late instars) was not affected by microclimate ($F_1 = 0.007$, $P = 0.979$). Fertilization treatments increased leaf-miner early-instar mortality (Wald $\chi^2 = 23.245$, $df = 1$, $P < 0.001$; C 91%, T1 98%, T2 98%) and parasitism rates (Wald $\chi^2 = 13.162$, $df = 2$, $P = 0.001$; Fig. 2). Moreover, parasitism rates were positively correlated with seasonal variation in foliar nitrogen ($t = 2.819$, $P = 0.009$, $R^2 = 21.5$). Parasitism rates were also related to microclimate (Wald $\chi^2 = 9.576$, $df = 1$, $P = 0.002$) and were higher at HD sites (Table 2). Further, the relative contribution of host-plant-related mortality vs. parasitism-based mortality was significantly related to microclimate ($\chi^2 = 16.796$, $df = 3$, $P < 0.001$), where parasitism contributed more to leaf-miner mortality at HD sites than at CW sites (Fig. 3).

Table 1 Summary of mixed-model repeated-measures ANOVA results for foliar nitrogen (percent dry mass) with elevation and treatment regime

Source of variation	Numerator <i>df</i>	Denominator <i>df</i>	<i>F</i>	<i>P</i> -value
Site	3	72	2.74	0.049
Treatment	2	72	4.59	0.013
Site×treatment	6	72	0.46	0.834
Date	2	144	206.36	< 0.001
Date×site	6	144	11.70	< 0.001
Date×treatment	4	144	2.46	0.048
Date×site×treatment	12	144	1.92	0.035
Contrast (effect)				
Microclimate	1	72	8.01	0.006
Control vs. treatments (1+2)	2	72	4.59	0.013
Treatment 1 vs. treatment 2	1	72	0.34	0.564
22 June vs. 25 July	1	144	37.27	< 0.001
25 July vs. 25 September	1	144	394.71	< 0.001

Table 2 Content (mean) and seasonal variation (SD between means across date) in percent foliar nitrogen (\pm SE) for elevations and microclimates [“cool/wet” (CW) and “hot/dry” (HD)]. E1 Elevation 2,192 m; E2 elevation 2,438 m; E3 elevation 2,635 m; E4 elevation 2,866 m

Microclimate	CW		HD	
	E2 2,438	E4 2,866	E1 2,192	E3 2,635
Foliar % nitrogen				
22 June	1.75 \pm 0.01	1.87 \pm 0.01	1.60 \pm 0.01	1.61 \pm 0.01
25 July	2.00 \pm 0.01	1.85 \pm 0.01	1.72 \pm 0.01	1.74 \pm 0.01
25 September	2.09 \pm 0.01	2.17 \pm 0.01	2.12 \pm 0.01	2.19 \pm 0.01
Annual	1.95	1.96	1.81	1.85
Seasonal variation in foliar % nitrogen (SD)	0.195		0.292	
<i>Phyllonorycter</i> sp. biomass (g/tree) ^a	0.17 \pm 0.01		0.09 \pm 0.01	
Parasitism rate ^b	8%		22%	

^a*Phyllonorycter* sp. biomass (g/per tree) for microclimate categories

^bParasitism rate represents the proportion of mines parasitized of the number available (late-instars only)

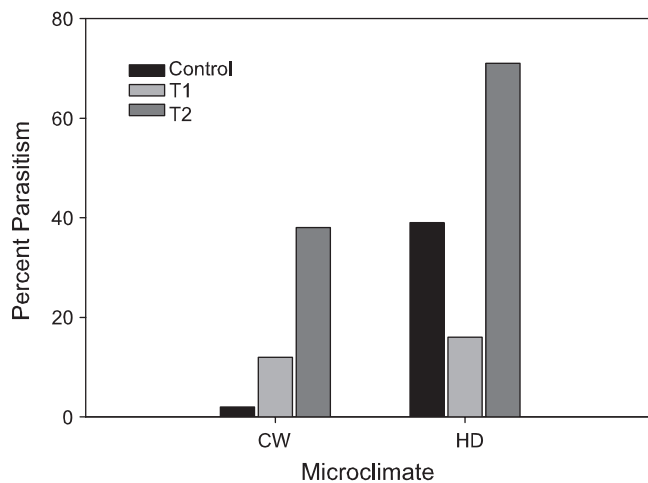


Fig. 2 Percent parasitism for treatment groups within microclimates. Percent parasitism represents the proportion of mines harboring parasitoids of the total mines available (late-instar only). T1 Treatment 1, T2 treatment 2; for other abbreviations, see Fig. 1

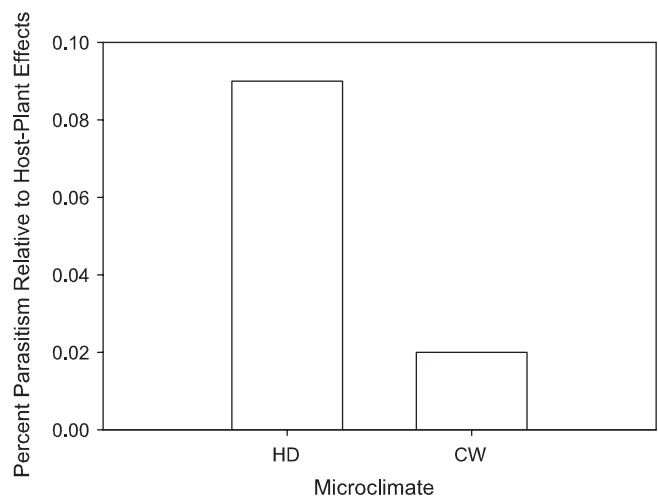


Fig. 3 Percent parasitism relative to host-plant effects (unexplained mortality) on *Phyllonorycter* sp. mortality across sites. Sites are enumerated according to elevation and re-ordered according to the first principal axis of environmental parameters. For abbreviations, see Fig. 1

Discussion

The conceptual “Chutes-and-Ladders” model of Hunter and Price (1992) emphasizes the role of biotic heterogeneity in the dynamic structure of tri-trophic interactions. In the Chutes-and-Ladders model, abiotic factors are integral to the production of the biotic heterogeneity at all trophic levels, subsequently affecting species interactions. Moreover, biotic forces (i.e., competition or predation) and abiotic variables (i.e., temperature or resource availability) may interact to further affect trophic interactions (see Moon et al. 2000; Gaston et al. 2004).

In this study, we found microclimate and fertilization to have significant effects on tri-trophic interactions in *Q. gambelii*. For *Q. gambelii*, local environmental conditions affected host-plant quality through changes in

the total amount of and seasonal variation in foliar nitrogen. Cooler, more humid sites (CW) were associated with a more predictable host—a host with lower seasonal fluctuation in foliar nitrogen and of better quality (higher total foliar nitrogen). Microclimate also affected rates of unexplained mortality—often attributed to host effects in leaf-miners (Preszler et al. 1996; Conner and Taverner 1997), where warmer drier sites (HD) experienced greater unexplained mortality.

Both microclimate and fertilization interacted with parasitoids of this system to affect parasitism risk for *Phyllonorycter* sp. At HD sites, *Phyllonorycter* sp. mines were at a greater risk of parasitism. Moreover, trees at those sites exhibit greater seasonal variation in foliar nitrogen which we found to be positively correlated to parasitoid attack. Fertilization treatments appeared to

have different effects between microclimates. The 50% nitrogen-demand treatment (T1) seemed to have a dampening effect on parasitism rates at the high-risk, HD microclimates, while parasitism rates increased on both control and 100% nitrogen-demand treatment groups at HD microclimates. Experimental nitrogen amendments elsewhere have revealed some evidence for increased parasitism risk on plants with experimentally adjusted nitrogen levels (Stiling and Rossi 1997; Moon et al. 2000). Unfortunately, detailed mechanisms of fertilization effects on parasitoid attack have not been reported for leaf-miners.

Phyllonorycter sp. survival and performance was also related to components of local microclimate (temperature, relative humidity) and fertilization. For *Phyllonorycter* sp., CW microclimates resulted in greater emergence success and biomass payoff. Yet, fertilization treatments had negative effects on *Phyllonorycter* sp. performance through increased early-instar mortality. Experimentally elevated levels of foliar nitrogen have been found to negatively affect leaf-miners in other species of oaks (Faeth et al. 1981). Moreover, fertilization treatments using inorganic nitrogen may alter mineral nutrition, amino acid balance, or potentially increase levels of toxic NO_3^- ions in foliar tissues (Karowe and Martin 1989; Clancy 1992). Measures of total elemental nitrogen alone do not elucidate these potential effects on *Phyllonorycter* sp. larvae. Of course, local microclimate may also have a direct effect on larval survival through changes in the abiotic environment (Andrewartha and Birch 1954) and our data suggest that leaf-miners may be more susceptible to microclimatic parameters than previously thought (Conner and Taverner 1997). Overall, our results suggest microclimate may affect geographical variation in the relative strength of trophic forces, and the addition of a second abiotic variable, such as microclimate may alter these spatial patterns of trophic dynamics.

Fine-scale combinations of abiotic components, or abiotic mosaics, affect many aspects of trophic interactions and, subsequently, spatio-temporal patterns in trophic dynamics (Preszler and Boecklen 1996; Brewer and Gaston 2002; Gaston et al. 2004). There has been no shortage of calls for further empirical study of environmental and geographic effects on species interactions (i.e., Hunter and Price 1992; Althoff and Thompson 2001; Hutchings et al. 2001), having been designated a primary "research frontier" in ecology (Thompson et al. 2001). However, studies incorporating spatio-temporal dynamics can be very difficult to implement and present considerable logistical obstacles. The difficulty of empirical studies of this type would only increase as one includes additional abiotic or biotic factors for consideration. This difficulty might be eased by concentrating experimental effort in areas of increased local variation in the abiotic (and thus biotic) environment, such as mountains, estuaries or riparian zones. Further, the effective use of these abiotic mosaics would be increased through the application of experimental gradients of

abiotic components across the mosaic. To summarize, we suggest that through careful experimentation utilizing abiotic mosaics, our understanding of the effects of environmental components on trophic interactions in terrestrial ecosystems will be more rapidly advanced.

Acknowledgements The authors thank Vince Gutschick, Ralph Preszler and Juha-Pekka Salminen for valuable advice and comments. This work was supported through a T & E Grant in Conservation Biology to C. T. Y. and NSF grants nos. DEB-129630 to W. J. B. and EPS-0132632 to New Mexico. This manuscript is dedicated to the memory of Dr Paul J. Currier, a formative force in the higher education of C. Y.

References

- Aguilar JM, Boecklen WJ (1992) Patterns of herbivory in the *Quercus grisea* × *Quercus gambelii* species complex. *Oikos* 63:498–504
- Althoff DM, Thompson JN (2001) Geographic structure in the searching behaviour of a specialist parasitoid: combining molecular and behavioural approaches. *J Evol Biol* 13:406–417
- Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. University of Chicago Press, Chicago, Ill.
- Benedict JH, Hatfield JL (1988) Influence of temperature-induced stress on host plant suitability to insects. In: Heinrichs EA (ed) Plant stress–insect interactions. Wiley, New York, pp 139–166
- Brewer AM, Gaston JG (2002) The geographic range structure of the holly leaf-miner. I. population density. *J Anim Ecol* 71:99–111
- Bryant JP (1987) Feltleaf willow–snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. *Ecology* 68:1319–1327
- Buse A, Dury SJ, Woodburn RJW, Perrins CM, Good JEG (1999) Effects of elevated temperature on multi-species interactions: the case of pedunculate oak, winter moth and tits. *Funct Ecol* 13:74–82
- Clancy KM (1992) Response of the western spruce budworm (Lepidoptera: Tortricidae) to increased nitrogen in artificial diets. *Environ Entomol* 21:331–344
- Conner EF, Taverner MP (1997) The evolution and adaptive significance of the leaf-mining habit. *Oikos* 79:6–25
- Dudt JF, Shure DJ (1994) The influence of light and nutrients on foliar phenolics and insect herbivory. *Ecology* 75:86–98
- Erelli MC, Ayres MP, Eaton GK (1998) Altitudinal patterns in host suitability for forest insects. *Oecologia* 117:113–142
- Faeth SH, Mopper S, Simberloff D (1981) Abundances and diversity of leaf-mining insects on three oak host species: effects of host-plant phenology and nitrogen content of leaves. *Oikos* 37:238–251
- Gaston JG, Genney DR, Thurlow M, Hartley SE (2004) The geographic structure of the holly leaf-miner. IV. effects of variation in host-plant quality. *J Anim Ecol* 73:911–924
- Hawkins BA, Cornell HV, Hochberg ME (1997) Predators, parasitoids and pathogens as mortality agents in phytophagous insect populations. *Ecology* 78:2145–2152
- Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732
- Hutchings MJ, John EA, Stewart AJA (2001) The ecological consequences of environmental heterogeneity. Blackwell, Oxford
- Karowe DN, Martin MM (1989) The effects of quantity and quality of diet nitrogen on the growth, efficiency of food utilization, nitrogen budget, and metabolic rate of fifth-instar *Spodoptera eridania* larvae (Lepidoptera: Noctuidae). *J Insect Physiol* 35(9):699–708
- Larcher W (1995) Physiological plant ecology, 3rd edn. Springer, Berlin Heidelberg New York

- Lull HW, Ellison L (1950) Precipitation in relation to altitude in central Utah. *Ecology* 31:479–484
- Mattson WJ Jr (1980) Herbivory in relation to plant nitrogen content. *Annu Rev Ecol Syst* 11:119–161
- Moon DC, Rossi AM, Stiling P (2000) The effects of abiotically induced changes in host plant quality (and morphology) on a salt marsh planthopper and its parasitoid. *Ecol Entomol* 25:325–331
- Moon DC, Stiling P (2003) The influence of legacy effects and recovery from perturbations in a tritrophic salt marsh complex. *Ecol Entomol* 28:457–466
- Mopper S, Simberloff D (1995) Differential herbivory in an oak population—the role of plant phenology and insect performance. *Ecology* 76:1233–1241
- Neilson RP, Wullstein LH (1986) Microhabitat affinities of Gambel oak seedlings. *Great Basin Nat* 46:294–298
- Oleksyn J, Modrzynski J, Tjoelker MG, Zytkowski R, Reich PB, Karolewski P (1998) Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Funct Ecol* 12:573–590
- Preszler RW, Boecklen WJ (1994) A three-trophic-level analysis of the effects of plant hybridization on a leaf-mining moth. *Oecologia* 100:66–73
- Preszler RW, Boecklen WJ (1996) The influence of elevation on tri-trophic interactions: opposing gradients of top-down and bottom-up effects on a leaf-mining moth. *Ecoscience* 3:75–80
- Preszler RW, Gaylord ES, Boecklen WJ (1996) Reduced parasitism of a leaf-mining moth on trees with high infection frequencies of an endophytic fungus. *Oecologia* 108:159–166
- Price PW (1992) The resource-based organization of communities. *Biotropica* 24:273–282
- Reynolds BC, Crossley DA Jr (1997) Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. *Environ Entomol* 26:1232–1239
- Roininen H, Price PW, Tahvanainen J (1996) Bottom-up and top-down influences in the trophic system of a willow, a galling sawfly, parasitoids and inquilines. *Oikos* 77:44–50
- Scriber JM, Slansky F Jr (1981) The nutritional ecology of immature insects. *Annu Rev Entomol* 26:183–211
- Sparks JP, Ehleringer JR (1997) Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects. *Oecologia* 109:362–367
- Stiling P, Rossi AM (1997) Experimental manipulations of top-down and bottom-up factors in a tri-trophic system. *Ecology* 78:1602–1606
- Thompson JN, Reichman OJ, Morin PJ, Polis GA, Power ME, Sterner RW, Couch CA, Gough L, Holt R, Hooper DU, Keesing F, Lovell CR, Milne BT, Molles MC, Roberts DW, Strauss SY (2001) *Frontiers in ecology*. *BioScience* 51:15–24
- White TCR (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63:90–105
- Xin XW (1993) Variation in foliar nitrogen concentration by forest type and climatic gradients in North America. *Can J For Res* 23:1587–1602
- Yarnes CT (2003) Abiotic factors affect herbivore preference–performance relationships in Gambel Oak (*Quercus gambelii*, Nutt.). MS thesis, New Mexico State University
- Yarnes CT, Boecklen WJ (2005) Abiotic factors promote plant heterogeneity and influence herbivore performance and mortality in Gambel's oak (*Quercus gambelii*). *Entomol Exp Appl* 114:87–95